A comparison of spinal ligaments—differences between bipeds and quadrupeds

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ABSTRACT

Following dissection, the spinal ligaments were observed in a selection of bipedal, pseudobipedal and quadrupedal animals during a search for an appropriate animal model for investigating the innervation of these ligaments. Midline spinal ligaments were found in all animals while lateral spinal ligaments could only be observed in bipedal (human) and pseudobipedal (avian) species. The presence of lateral spinal ligaments in these animals and their absence in quadrupeds suggests that the development of the lateral ligaments reflects a mechanical challenge unique to the erect spine and that these lateral spinal ligaments are fundamental to the stability of an erect posture.

Key words: Spine; spinal ligaments; scoliosis; bipedalism; quadrupedalism.

INTRODUCTION

Spinal ligaments are important structures for maintaining the stability of the spine as they provide both simple mechanical constraint and neuromuscular feedback (Yahia et al. 1988; Rhalmi et al. 1993). As a mechanical structure, a ligament has to be stretched before it can provide support and consequently the mechanical function of a spinal ligament depends on its attachments and their position relative to the centre of rotation of the spine. For example, the supraspinous and interspinous ligaments which are located in the midline and posterior to the rotation axis control flexion of the spine (Panjabi & Goel, 1982) whereas the superior costotransverse ligaments (SCTL), located in the lateral region of the spine, are found to be more important in maintaining balance of the spine in the coronal plane. Mechanically, the SCTL with its lateral attachments has been shown to be more effective in producing lateral force than those ligaments that are attached solely in the midline and which are unable to produce lateral force (Jiang et al. 1994). Furthermore, it has been shown that severing the SCTL in the rhesus monkey results in development of scoliosis (Thomas & Dave, 1985) which accords well with concepts of scoliosis development dependent on ligament involvement according to methods of mechanical modelling of the spine (Lindahl & Raeder, 1962; Schultz et al. 1972). Consequently, it has been hypothesised that asymmetry in the mechanics of the lateral spinal ligaments could be related to the aetiology of diseases such as idiopathic scoliosis where lateral curvature and vertebral rotation are prominent features (Jiang et al. 1995).

Having recently demonstrated the importance of the lateral ligaments of the spine by mechanical modelling, particularly SCTL, to the maintenance of an erect posture in humans and its potential significance in scoliosis (Jiang et al. 1995), attempts were made to identify an appropriate animal model to use as the basis for further study. A review of the literature revealed only sparse details of the lateral spinal ligaments for only a few individual animals. From some initial dissections of a variety of species it quickly became evident that there was great variation in these ligaments between different animals. Accordingly a detailed comparative study of spinal ligaments was undertaken. The results showed that while all the animals studied possessed the central spinal ligaments such as the supraspinous and inter-

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spinous ligaments, they did not all possess the lateral spinal ligaments such as SCTL. Specifically, the quadrupedal animals (e.g. dog, rat, cat) did not possess the lateral ligaments whereas the bipedal (man) and pseudobipedal (e.g. chicken, duck, turkey) possessed well defined lateral ligaments. It is suggested that the development of the lateral ligaments is a consequence of an upright posture.

MATERIALS AND METHODS

Spines from a variety of different animal species, including man, were obtained either from the Department of Anatomy and Cell Biology (human spines) or from the University Farm, University of Alberta (see Table). Most of the spines were from mature animals but in some cases (e.g. chickens) immature spines were also collected for comparison. Similar results were observed both in immature and mature specimens and further comparison was discontinued in this study. The spinal ligaments from thoracic level T7 to T11 for the mammals and from T3 to T6 for the birds were exposed by careful dissection. These levels represent the lower thoracic regions in these species and are where the lateral spinal ligaments are most prominent. They also represent regions of the spine in which there is a high prevalence of scoliosis. The central spinal ligaments, consisting of the supraspinous and interspinous ligaments (SSL/ISL), were exposed posteriorly by cutting the skin and removing the subcutaneous tissue. Similarly, the intertransverse ligaments were exposed by further dissection of the trapezius, latissimus dorsi, semispinalis thoracis and levatores costarum muscles. Special care was taken to notice any other ligamentous tissue between the transverse processes. The SCTL were exposed through an anterior approach in which the pleura was first removed as well as the underlying loose connective tissue.

Table. *Comparison of spinal ligaments between different species**

Locomotion	Animal	No.	SSL/ISL	ITL	SCTL
Bipedal	Human	32	+	−	+
	Chick	10	+	+	+
	Turkey	3	+	+	+
	Duck	1	+	+	+
Quadrupedal	Pig	10	+	−	−
	Dog	2	+	−	−
	Cat	2	+	−	−
	Rat	8	+	−	−
	Mouse	5	+	−	−
	Hamster	10	+	−	−

* Although ligaments were simply identified with '+' for present and '−' for absent, the SSL/ISL in the quadrupeds were generally less well developed.

Having exposed the spinal ligaments, their absence or presence was noted and a brief description was made of their morphology as they appeared under a dissecting microscope. In cases where ligaments were found to be absent on initial observation, further dissection was performed to ensure that no other extraneous ligamentous tissue was present.

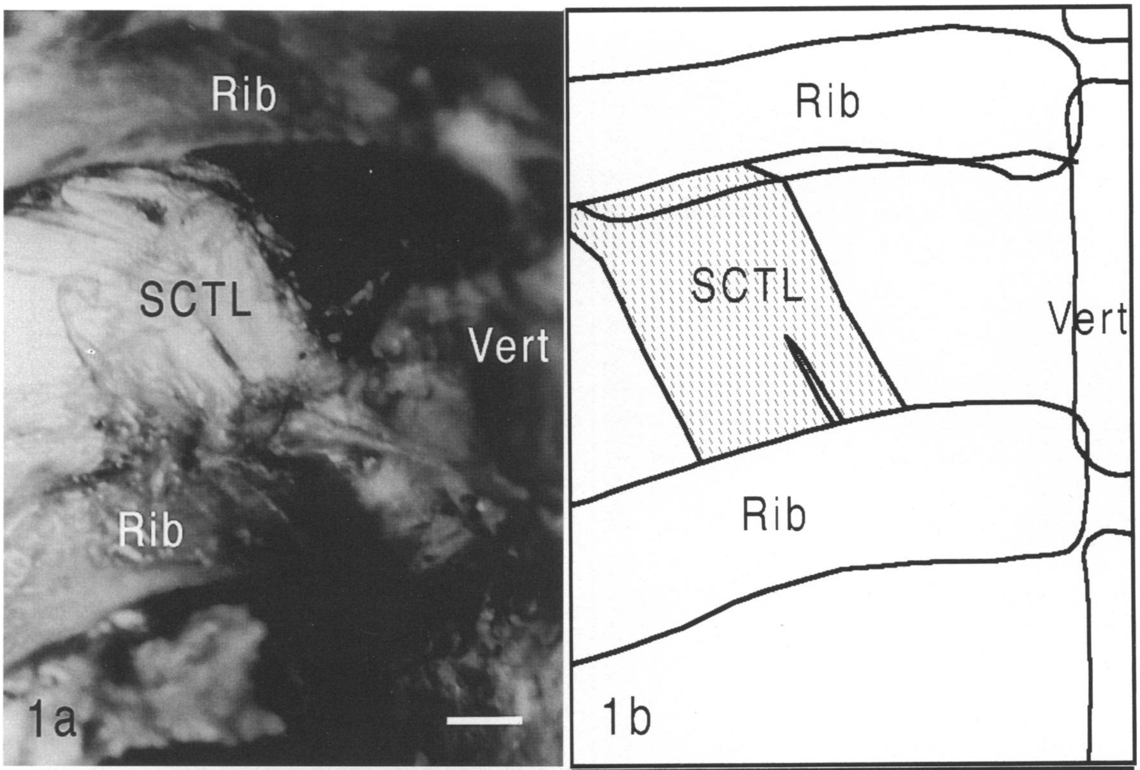
Initially, the results from the dissections of the individual species were kept separate but it became apparent that a pattern developed if they were grouped in accordance with their method of pedal locomotion: bipedal (human), pseudobipedal (avians) (Thorp, 1989) or quadrupedal (pig, dog, cat, rat, mouse, hamster).

RESULTS

The presence or absence of the various spinal ligaments and the descriptions of their morphology were consistent within each of the separate species with little individual variation. Similarly, there was consistency within the groupings as shown in the Table. The results are therefore described in relation to the groupings shown.

Observations from bipeds (humans)

In all cases, the SSL/ISL complex, which represents the central spinal ligament, was very prominent in the midline, firmly connecting the adjacent spinous processes. The ligament was extremely tough and extended along and between the full length of the superior and inferior borders of the spinous processes as well as being thickened between the tips of the processes. It was difficult to determine a precise border between the SSL and ISL as there was a gradual merging of the tissues in these regions, but the free edge of the ligament, between the tips of the spinous processes, was thickened and was taken to represent the SSL. In contrast, it was found that the only lateral spinal ligament connecting adjacent vertebrae was the superior costotransverse ligament (SCTL). The SCTL passed laterally from the sharp crest on the superior border of the neck of the rib (costal process of the vertebra) below to the lower border of the transverse process of the vertebra immediately above (Fig. 1). This was a well defined, tough tissue clearly separate from adjacent tissues and



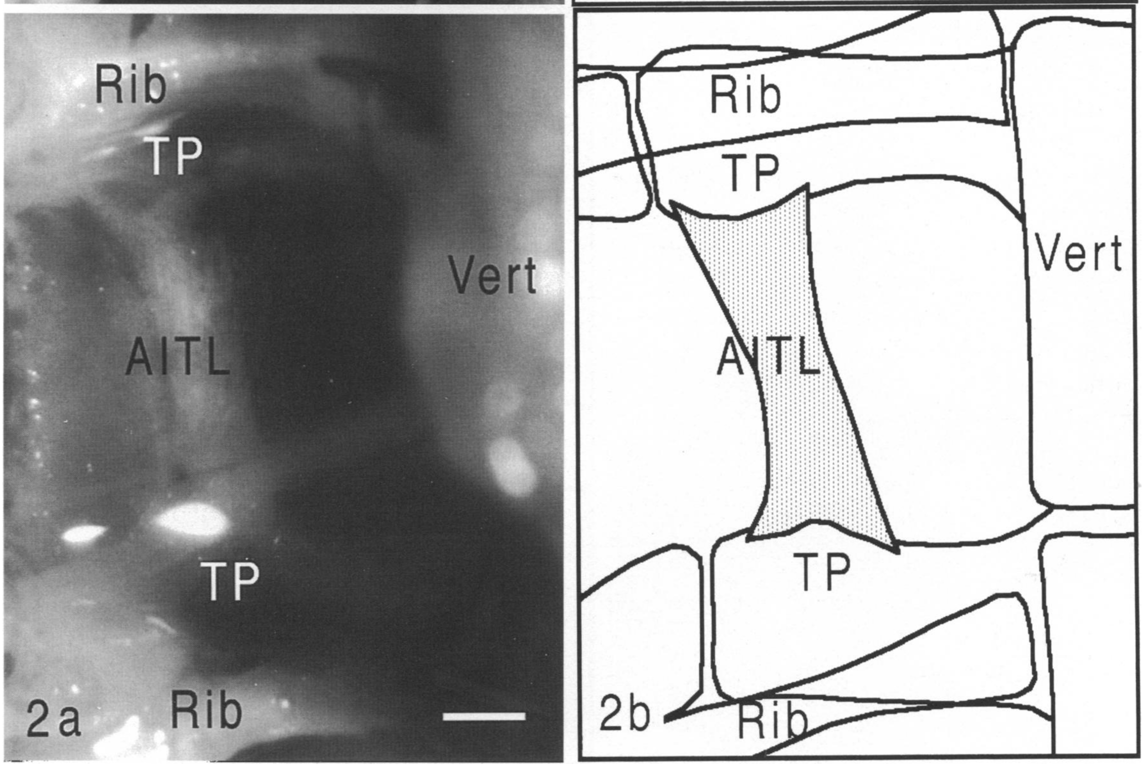
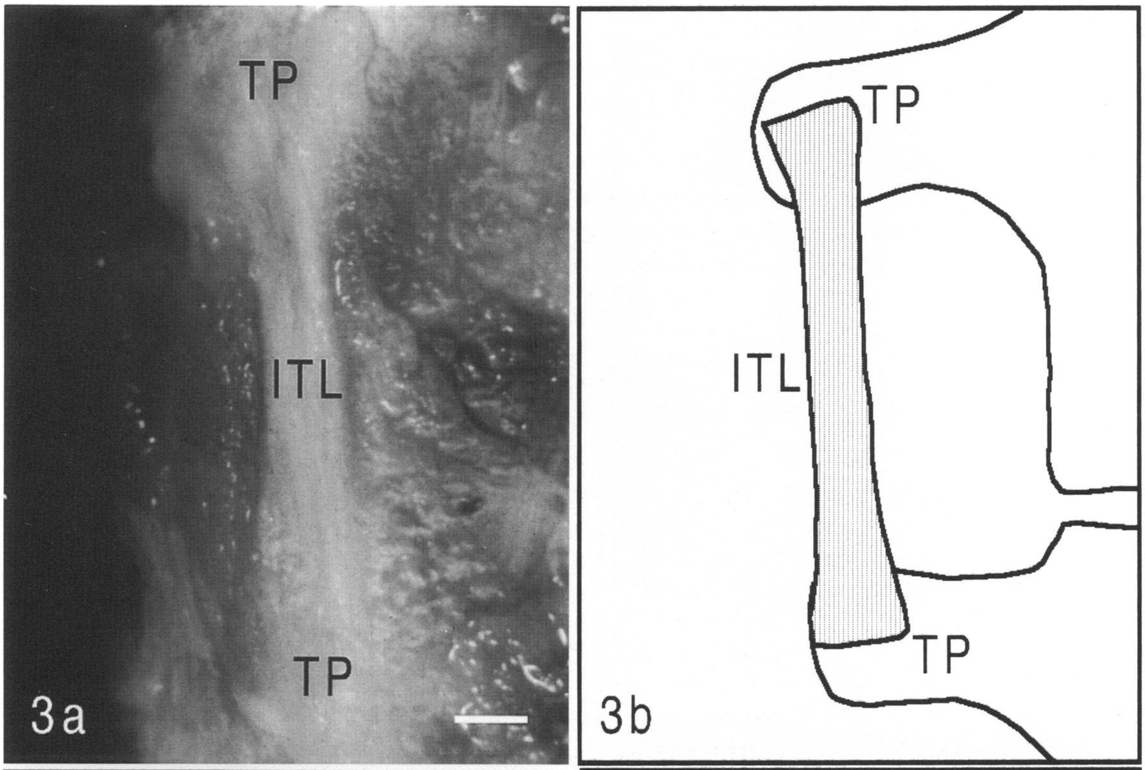


Fig. 1. (*a*) Photomicrograph (anterior view) showing a typical superior costotransverse ligament in a human specimen. The ligament is a thick and dense band on the lateral side of the vertebra. (*b*) Explanatory drawing. Vert, vertebral body; SCTL, superior costotransverse ligament. Bar, 2.5 mm.

Fig. 2. (*a*) Photomicrograph (anterior view) showing the anterior intertransverse ligament found in a young chicken. This ligament has similar sites of attachment as the SCTL in man. The ligament becomes more prominent as the chicken gets older but is already well pronounced even at this young age. (*b*) Explanatory drawing. TP, transverse process; AITL, anterior intertransverse ligament; Vert, vertebral body. Bar, 1 mm.



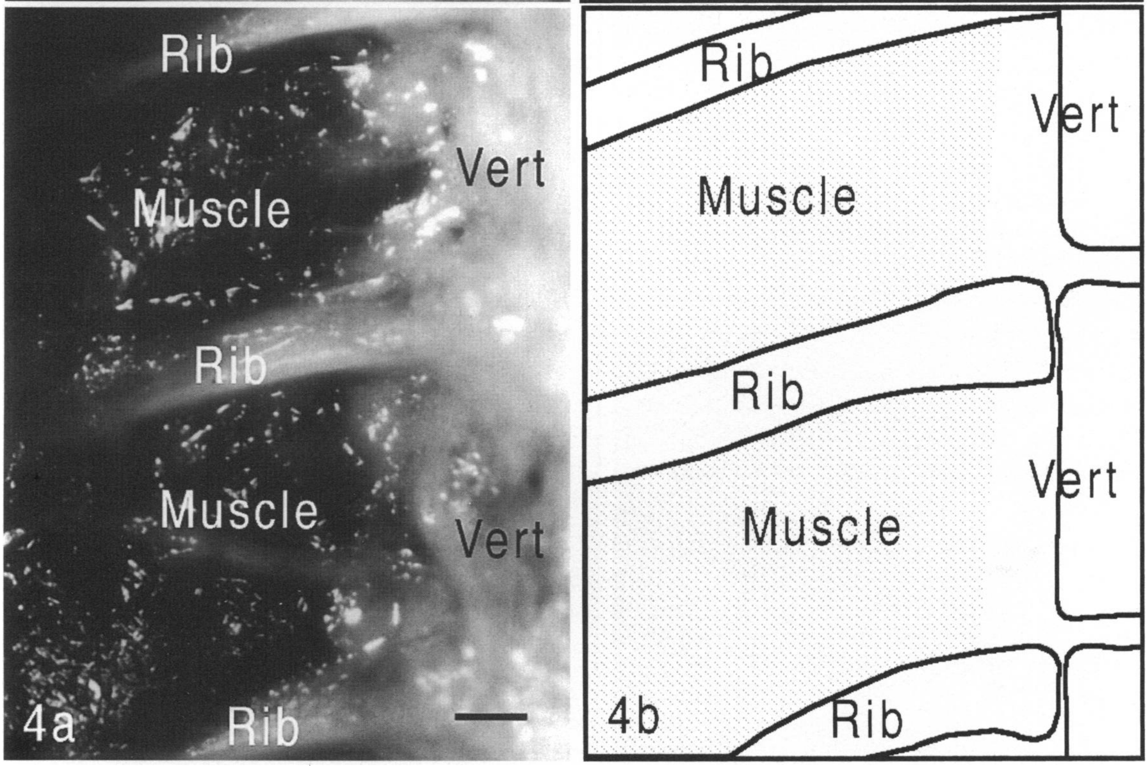


Fig. 3. (*a*) Photomicrograph of the posterior region of the spine in a young chicken. The intertransverse ligament is a well defined ligament which connects 2 transverse processes. This ligament is also absent in quadrupedal animals. (*b*) Explanatory drawing. TP, transverse process; ITL, intertransverse ligament. Bar, 1 mm.

Fig. 4. (*a*) Photomicrograph of the costovertebral region of a rat. No ligamentous tissue could be found among the abundant muscles. (*b*) Explanatory drawing. Vert, vertebral body. Bar, 1 mm.

was very prominent. The ligament blended laterally with the internal intercostal membrane while the medial border formed a free edge. The orientation of most of the ligament fascicles was from superolateral to inferomedial except for a small bundle of fascicles that ran inferolaterally to the rib below. No obvious posterior layer was identified. The intertransverse ligament (ITL), a commonly described ligament (Williams et al. 1989) in the lumbar region, was found not to be a ligament at all in the thoracic region but simply the interweaving of the tendons of adjacent muscles. The results relating to the SCTL and ITL in man have been presented in more detail in an earlier paper (Jiang et al. 1995).

Observations from pseudobipeds (avians)

The central spinal ligaments (SSL/ISL complex) were found to be prominent in all species and similar to that already described for the true bipeds (man). Further detailed description is unnecessary and has thus been omitted. However, 2 lateral spinal ligaments were found in the avians, an anterior intertransverse ligament (AITL) and an intertransverse ligament (ITL). The AITL was a membrane-like structure with thickening in the lateral aspect (Fig. 2). The collagenous fascicles were oriented obliquely from the lateral part of the transverse process of the upper vertebra to the middle part of the transverse process of the lower vertebra. This orientation of the ligament is similar to that of the SCTL described for man and therefore was considered the equivalent to the SCTL in man. The ITL was a dense, band-like structure which was oriented parallel to the long axis of the spine and was attached between the posterior lateral part of the upper and lower transverse processes of adjacent vertebrae (Fig. 3). It too was a prominent structure. It connected to the AITL anteriorly and was surrounded by paraspinal muscles in other aspects.

Observations from quadrupeds (pig, dog, cat, rat, mouse, hamster)

The central spinal ligaments (the SSL/ISL complex) were clearly defined in quadrupeds. The SSL/ISL were attached to adjacent supraspinal processes and were of a similar nature to those already described above for both the bipeds (man) and pseudobipeds (avians). However, these ligaments were less thick and tough compared with those of human or avians. In sharp contrast, no lateral spinal ligaments were found to connect adjacent vertebrae or their transverse processes in any of these species although abundant intercostal muscles were found (Fig. 4).

In summary, it is clear from the Table that all species possessed very clear and prominent central spinal ligaments (SSL/ISL) but that the presence of lateral spinal ligaments (SCTL or ITL) was restricted to bipedal and pseudobipedal species.

DISCUSSION

Although spinal ligaments have been well studied in man (Williams et al. 1989), descriptions of the spinal ligaments in other animals have apparently not been well documented other than for a brief study of the SSL/ISL in dog, cat and baboon (Heylings, 1980) and a comparison of the iliolumbar ligament in both bipeds and quadrupeds (Pun et al. 1987). In particular, there does not appear to have been any study dedicated to the lateral thoracic spinal ligaments. In this study, we found that all species studied possessed prominent central spinous ligaments although they were less well developed in the quadrupeds. In contrast, only the bipeds (man) and pseudobipeds (avians) possessed lateral spinal ligaments. In the quadrupeds, the absence of lateral spinal ligaments was conspicuous. The appearance of lateral spinal ligaments only in bipedal animals suggests that they may be important in supporting the spinal column for a bipedal stance although other functions are also possible and should be considered.

It is significant to note that the SCTL was well developed in man and bipedal animals but was absent in the quadrupeds. It has been suggested that the erect posture of the human spine requires considerable ligamentous support and that lateral support is fundamental in keeping the spine straight in the sagittal plane (Lindahl & Raeder, 1962; Schultz et al. 1972). Furthermore, the bipedal gait of man constantly rotates the trunk and tilts the pelvis thereby requiring increased lateral support to remain balanced (Townsend & Seireg, 1972; Gracovetsky, 1985; Marks, 1987). In particular, this form of locomotion will disturb the balance of the spine laterally and cause stress in the lateral structures of the spine. Conversely, the spine would be more unstable and prone to development of deformity if it was forced into maintaining an erect posture without proper structural adaptation. Such development of spinal deformity was reported by Tanaka et al. (1982) who observed both bipedal and quadrupedal rats fed with semicarbazide. He found that the frequency of occurrence of scoliosis was 82% in the bipedal rats and 13% in the quadrupedal rats. This significant increase in the development of scoliosis was attributed to the forced erect posture in the bipedal rats for a spine which was designed for a prone posture although it is possible that the experimental procedure used to create the bipedal rats would have made the spine inherently unstable without the evolutionary changes accompanying the development of an erect posture. Similarly, the costotransverse ligament has been reported to be present in the rhesus monkey which appears to have a dual method of locomotion. However, cutting of the costotransverse ligaments on one side results in the development of scoliosis (Thomas & Dave, 1985) presumably through removal of the lateral supportive forces for the vertebral column. The finding in this study that the lateral spinal ligaments are found only in those species that walk in a bipedal fashion with an erect posture suggests strongly that these ligaments are critical for the maintenance of an erect spine and that their absence or malfunction could lead to the development of spinal deformity such as is found in scoliosis where lateral instability and abnormal vertebral rotation are prominent features.

The evolution of spinal ligaments has been attributed to the biomechanical load of the spine (Pun et al. 1987) and therefore analysis of the load pattern of the spine could help in understanding the function of the spinal ligaments. The load pattern on the spine is dramatically changed from the prone posture to erect posture. In a bipedal stance, the spine acts as a column which is more liable to instability and needs to be balanced in both the sagittal and coronal planes (Lindahl & Raeder, 1962; Schultz et al. 1972; Cappozzo, 1983) whereas in a quadrupedal stance the spine functions as a suspension mechanism. Based on these models, some developmental adaptations of the spinal ligaments have been suggested and identified. For example, Heylings (1980) reported that in the lumbar region, the dog and cat had only thin and poorly defined SSL/ISL. It was suggested that instead of needing to stabilise their spines, these quadrupeds needed to flex and extend greatly their lumbar spines to provide and accommodate for their running gait. In contrast, the strong collagenous SSL/ISL in man can give good control of flexion of the spine during movement in a bipedal stance (Heylings, 1980). The results of the present study suggest that similar adaptations might have occurred in the erect spine of bipeds with regard to the stabilising functions of the lateral spinal ligaments.

It is interesting to note that the iliolumbar ligament also was found only in bipeds and was absent in quadrupeds (Luk et al 1986; Luk & Leong, 1987), a finding similar to that for the lateral spinal ligaments investigated in this study. Specifically, the iliolumbar ligament was absent at birth in man and only attained 'full' differentiation in the 2nd decade after birth (Luk et al. 1986). It was suggested that the stress across the lumbosacral junction as a result of the erect posture played an important role in stimulating the formation of the iliolumbar ligament and was not complete until puberty. The results of the current study suggest that an upright posture in the bipedal and pseudobipedal stance is related to the development of lateral spinal ligaments which are so conspicuously absent in quadrupeds. Development of these ligaments during growth particularly in relation to acquisition of the upright stance warrants further study.

While Marks (1987) suggested that hominid bipedalism is a learned behaviour, this study and those of others (Heylings, 1980; Luk et al. 1986; Pun et al. 1987) have described several structural adaptations of the human spine that appear to be related to the maintenance of an upright posture. Clearly, failure to balance the erect spine may cause problems such as idiopathic scoliosis. From reviewing the literature, it is significant to note that quadrupeds do not appear to develop idiopathic scoliosis naturally while there are many reports of avian models for idiopathic scoliosis and adolescent idiopathic scoliosis is not uncommon in man (Rogala & Drummond, 1978). This difference might be attributed to the prone posture and locomotion pattern of the quadrupeds which does not apply the type of loads that challenge the lateral stability of their spine. In contrast, weight bearing and the dynamics of bipedal locomotion make the spine liable to lateral instability. In this regard, the chicken with its pseudobipedal stance and form of walking has been reported to develop idiopathic scoliosis (Rigdon & Mack, 1968; Machida et al. 1994) and, coupled with the presence of well defined and prominent lateral spinal ligaments, could be an ideal animal model to examine the role of lateral spinal ligament in the lateral balancing of the spine and the development of idiopathic scoliosis.

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